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REVIEWS

Letter

Contrary to the Gospel, Ravens Do Plan Flexibly

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The Gospel of Luke proclaims that ravens do not plan for the future; instead, God provides for them. However, in a recent study (Box 1) we showed that ravens are capable of domain-general planning, also called flexible planning, which we define as making decisions about futures outside one's current sensory scope in domains for which one is not predisposed [1]. We subjected ravens to two such domains – token exchange with humans and tool use – that have also been studied with great apes and monkeys (e.g. [2,3]). The results strongly suggested that ravens' actions were directed towards future, rather than immediate, rewards. Importantly, we sought to learn more about the deep natural history of cognition by charting behavioural complexities in birds, hitherto reported only for great apes. We investigated functional aspects of raven planning in comparison to apes; that is, whether they use similar operationally defined cognitive functions, such as self-control and long-term memory.

Redshaw and colleagues recently published a critique of our paper [4]. In doing so, they have adopted a line similar to the ancient gospel, but with associative learning as the ravens' main provider. However, we worry that their critique risks distorting the aim of our research. In particular, they examined our results through a lens of human uniqueness by implying that planning exists only in the humanesque form of episodic memory mechanisms. Because they interpreted our claims about function as claims about mechanism, Redshaw *et al*. ended up criticising a straw man. The authors also misunderstood our methods, and offered a hard-to-grasp associative learning account or – puzzlingly in our opinion – a planning mechanism as alternative explanations for our results.

In their commentary, Redshaw and colleagues seem to suggest that we investigated planning for an event at a specific future time. We did not. Rather, we used their own nonlinguistic criteria for basic planning, which are also related to Köhler's and Tulving's criteria [5–8]. This is about demonstrating a long-term memory of a specific event, but does not involve demonstrating planning for a particular future time (although in their commentary Redshaw *et al*. suggest that the 'specific future occasion' criterion is articulated in the paper they cite [6]). In other words, one plans from a memory-based expectation rather than from knowledge about precisely when the situation will occur: if you have experience of the London weather and – after glancing at the dark skies – grab an umbrella before leaving the hotel, it does not mean that you know it will rain at 10 o'clock or that it will rain at all. You plan based on long-term memory and expectations.

We also worry that readers may come away from Redshaw and colleagues' commentary with the impression that ravens went directly from training to selecting the correct items on the first test trial, a behaviour that they claim might be suggestive of associative learning since, according to this account, ravens lacked repeated experience of the future event. However, this description jumps an essential step: ravens did not go directly to the first trial. An hour before the trial, they encountered a situation where either a tool or an exchangeable item was needed although they had none. This method is in keeping with influential planning criteria from Köhler [7] to Tulving [8]: experiencing a rainy day without an umbrella. The ravens solved the task after this first experience, giving no reason to think they would not do so after repeated exposures. Why repetition would better demonstrate long-term memory of a single event is unclear.

One of Redshaw *et al*.'s suggestions was that rather than knowing the items' function, ravens regarded them as valuable only in themselves (also known as implicit associative learning [9]). However, we explored whether the ravens' decisions relied on the expectation that they would be immediately rewarded (predicted by implicit associative learning). We performed two self-control experiments with different delays – an established method to evaluate the influence of time on the subjective value of rewards. If one's cognition is sensitive to delays, it is more difficult to exert self-control when the reward is temporally further away. Such sensitivity demonstrates that preference for the goal-directed item does not result from implicit associative learning, as it carries more than intrinsic value.

Critically, when the delay was 15 min, ravens selected the future-directed item over a small immediate reward in 73.5% of trials (compared with 96.5% when no immediate reward was present with the same delay). When the reward was less than 1 min away, the selection rate rose to 100%. The difference between the delays was significant on both the individual and the group level, using a group comparison of two sets of 98 trials each. No learning curve was detected. We concluded that the items were not intrinsically rewarding.

Of course, one might object, as Redshaw and colleagues seem to, by suggesting that the ravens did not recognize the delay (and exerted no self-control). However, then one must explain why ravens now failed 26.5% of trials compared with 3.5% when no immediate reward was present. Such large differences are predicted by self-control, but not from an account where the item carries intrinsic

Box 1. The Setup of the Study

The study [1] comprised four experiments, each with two conditions that were chosen to preclude behavioural predispositions of ravens: token exchange with humans and tool use (ravens are non-tool users in the wild). Before the experiments, the ravens learned to use the tool not through associative learning but from a single observation, and repeated this successfully five times (the only times they had ever used tools). They learned to exchange the correct token in less than 30 trials. The training deviated from the testing, as they never selected the items among distractors and the apparatus or exchanging human was present. Importantly, they never experienced the problem they had to plan for until after training: a situation where an item was needed but they had none [7,8]. The experiments replicated previous studies with primates, but also included new controls. Experiment 1 tested decision-making for 15 min into the future while Experiment 2 tested for 17 h. Experiment 3 tested self-control in a 15-min setting and Experiment 4 in a <1-min setting. The results of these experiments were compared to evaluate the value of the items. All individuals performed significantly above chance *per* planning criteria in all experiments and conditions.

value. Further, one would have to assert that in the 15-min delay experiment the ravens associatively learned – in a handful trials each week – that the item was more rewarding than the immediate reward and that this learning had no signature learning curve, such that they instantly became 100% successful with the short delay. Such learning – if there were any trace of it – sounds like learning used in planning, which involves forming associations between long-term memories of events. This is no lean learning explanation, and hardly any alternative to planning.

The other alternative explanation provided by Redshaw and colleagues was that the ravens used memory-mediated reinforcement, or mnemonic associations. This is a peculiar argument, as mnemonic associations are dependent on episodic memory and are regarded as one alternative to Mental Time Travel planning, but not as an alternative to planning *per se* [10]. Mnemonic associations occur where the animal at the future situation recollects the actions that led to that situation (actions initially driven by goal-directed associative learning or innate propensities) and so learns this connection, which later drives planning behaviour in similar situations.

Such a planning mechanism does not work, however, with respect to past actions not directed towards the future reward: in this case, selecting the immediate reward. Then, the animal must already know that the selection event is future related, otherwise it could have associated any action, at any time, that failed to lead to the reward [11]. So, if mnemonic associations were used, the ravens must have known the item–outcome relationship before the self-control experiments, making our control valid anyway. Given the results it is improbable that such associations were at play, but if they were they are still no alternative to planning.

The fact that ravens exert future-oriented behaviours, apparent in apes and mature humans but not in monkeys or young children, does not vanish with attempts to recharacterise planning terminology. That merely diverts from the intriguing theoretical consequences that arise from the discoveries that some avian dinosaurs parallel the complex behaviours of our closest relatives and us.

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Forum

Stressful Events as Teaching Signals for the Brain

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Stressful events are better remembered than mundane events. We explain this advantage by reconceptualizing stress in terms of cumulative prediction errors (PEs) that promote rapid learning of events. This proposal integrates the effects of stress on perception and memory, and provides exciting new perspectives for research on stress and cognition.

Stress is ubiquitous in our daily life and can have a major impact on our mental health and wellbeing. This impact may in part be driven by stress-induced changes in cognition. In particular, it is well documented that stressful events are typically much better remembered than mundane events. Enhanced memory for stressful events may be highly adaptive as it prepares us